Maxent modeling for predicting the potential geographical distribution of two peony species under climate change

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HIGHLIGHTS

- Species distribution modeling was used to predict the distribution of *Paeonia delavayi* and *P. rockii.*
- Temperature seasonality and isothermality were the most critical factors shaping *P. delavayi* distribution.
- UVB-4 and annual precipitation were the most critical factors for shaping *P. rockii* distribution.
- Both species showed range expansions towards higher elevation.

GRAPHICAL ABSTRACT
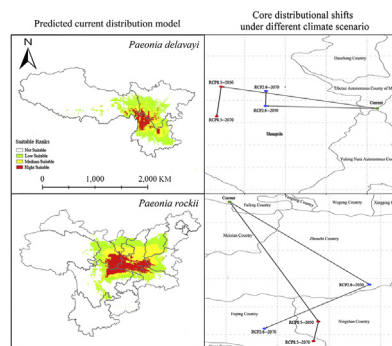
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ABSTRACT

Paeonia (Paeoniaceae), an economically important plant genus, includes many popular ornamentals and medicinal plant species used in traditional Chinese medicine. Little is known about the properties of the habitat distribution and the important eco-environmental factors shaping the suitability. Based on high-resolution environmental data for current and future climate scenarios, we modeled the present and future suitable habitat for *P. delavayi* and *P. rockii* by Maxent, evaluated the importance of environmental factors in shaping their distribution, and identified distribution shifts under climate change scenarios. The results showed that the moderate and high suitable areas for *P. delavayi* and *P. rockii* encompassed ca. 4.46×10^5 km^2 and 1.89×10^5 km^2, respectively. Temperature seasonality and isothermality were identified as the most critical factors shaping *P. delavayi* distribution, and UVB-4 and annual precipitation were identified as the most critical for shaping *P. rockii* distribution. Under the scenario with a low concentration of greenhouse gas emissions (RCP2.6), the range of both species increased as global warming intensified; however, under the scenario with higher concentrations of emissions (RCP8.5), the suitable habitat range of *P. delavayi* decreased while *P. rockii* increased. Overall, our prediction showed that a shift in distribution of suitable habitat to higher elevations would gradually become more significant. The information gained from this study should provide a useful reference for implementing long-term conservation and management strategies for these species.

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1. Introduction

The Fifth Assessment Report (AR5) produced by the Intergovernmental Panel on Climate Change (IPCC) states that global warming is expected to continue with the average temperature of earth increasing

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by 0.3–4.5 °C by 2100 compared with 1986–2005 (Stocker et al., 2013). Climate change has caused substantial changes in the geographical distribution of many species. In turn, changes in species' ranges will affect how climate change is experienced across the landscape because surface vegetation strongly affects atmospheric properties (Thuiller et al., 2005; Fitzpatrick et al., 2008; Lawler et al., 2009).

Various species distribution models (SDMs), such as CLIMEX, Domain, genetic algorithm for rule set production (GARP), and maximum entropy (Maxent), have been used to evaluate the ecological requirements, ecological responses, and distribution areas (Guisan and Thuiller, 2005; Phillips and Dudík, 2008). Among these modeling approaches, Maxent is widely used since it performs better with small sample sizes relative to other modeling methods (Pearson et al., 2007; Phillips and Dudík, 2008) [see Elith et al., 2006 and Tsoar et al., 2007 for a more detailed comparison of various SDMs]. For example, Phillips et al. (2006, 2009) found that Maxent outperformed GARP on observation data for North American breeding birds and for two Neotropical mammals (*Bradypus variegatus* and *Microryzomys minutus*).

Paeonia, the only genus in the Paeoniaceae, has been used by humans for >2000 years and as a traditional floral symbol of China. It is known as "king of the flowers", and is used symbolically in Chinese art (Hong and Pan, 1999; Zhou et al., 2014). In addition to the aesthetic value, peony plants have been an important source of crude drugs in traditional Chinese medicine. Many peony species have a wide range of uses, and thus, have been subjected to unsustainable rates of harvest. Hong et al. (2017) reviewed the status of wild tree peony species based on the field surveys. They found that most wild tree peonies are endangered and *P. cathayana* and *P. ostii* each survive as only one lone individual.

If biological and environmental data is not available for peony species, developing a scientifically-sound conservation strategy and related conservation measures will be difficult (Hong et al., 2017). Another crucial issue related to the ecological importance and economic significance of peony species is to determine how climate change will affect the spatial extent of their suitable habitat. However, researchers have yet to fully understand the ecological requirements and identify priority areas for restoration of tree peony species based on current and future climatic scenarios.

To evaluate the properties of habitat distribution and environmental factors shaping suitability of habitat, we used Maxent modeling to predict distributions of two peony species (*P. rockii* and *P. delavayi*) in China using an extensive collection of geo-referenced occurrence records and recent surveys. The objectives of the present study include: (1) identifying the most important environmental factors that affect the ranges of these two species, (2) examining the spatial extent of suitable habitat for these species using various scenarios that model the nature and trends of changes in current and future climate, and (3) quantifying the spatial patterns of changes in the extent of suitable habitat using future climate conditions in a way that will facilitate the development of appropriate conservation measures.

2. Material and methods

The full workflow on which analyses were based is summarized in Fig. 1.

2.1. Occurrence collection

To obtain the occurrence records for *P. delavayi* and *P. rockii* across their whole ranges, we conducted an extensive literature search using online databases and referred to the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/) and the Chinese Virtual Herbarium databases (CVH, http://v5.cvh.org.cn/). When occurrence records lacked exact geo-coordinates, we used Google Earth (http://ditu. google.cn/) to determine the latitude and longitude. Using the above sources, the distributional localities of *P. delavayi* and *P. rockii* were

compiled into a database. Duplicate records were deleted and filtered spatially so that only one point occurred within each grid cell (10 km × 10 km). With the help of ArcGIS 10.2 (Esri, Redlands, California USA), a sighting point map was developed. A total of 122 and 69 documented presence records of *P. delavayi* and *P. rockii*, respectively, were obtained for constructing the models (Fig. 2).

2.2. Environmental parameters

We initially selected 29 environmental factors that may influence the distribution of *P. delavayi* and *P. rockii* to model the current species distribution patterns. These included 19 bioclimatic variables with 30 s (ca. 1 km) spatial resolution obtained from the World Climate Database (www.worldclim. org) (Hijmans et al., 2005), growing degree days (GDD), soil pH (SpH) and soil organic carbon (SC) from the Center for Sustainability and the Global Environment (http://www.sage.wisc. edu/atlas/index.php) (New et al., 1999); ground-frost frequency (FRS), wet-day frequency (WET), and vapor pressure (VAP) from the IPCC database (http://www.ipcc-data.org/obs/cru_ts2_1.html); and global UV-B radiation (UVB1–4) from the gIUV database (http://www.ufz.de/gluv/) (Beckmann et al., 2014).

For future climate scenarios, we used BCC-CSM1.1 climate change modeling data under the Representative Concentration Pathway (RCP) 2.6–2050, RCP 2.6–2070, RCP 8.5–2050 and RCP 8.5–2070 scenarios released by IPCC Accessment Report 5 (AR5). BCC-CSM1.1 is among the most-used models currently available for simulating the global climate response to increasing greenhouse gas concentration. Our four selected future climate data sets were downloaded from the World Climate Database (Hijmans et al., 2005). The 10 environmental parameters (SC, SpH, GDD, FRS, WET, VAP and 4 UV-B radiation parameters) remained unchanged following the analyses of SDM projection under future climate conditions.

These environmental parameters were preprocessed to a general spatial resolution of 30″ latitude/longitude (ca. 1 km² at ground level). Many of the bioclimatic variables are spatially correlated. To avoid multicollinearity of variables that can result in model over-fitting (Graham, 2003), we used Spearman's rank correlation to examine the cross-correlation (Spearman's < 0.75) and removed highly correlated environmental factors. Out of 29 variables, only 17 were selected as evaluator variables (Table 1).

2.3. Current and future potential habitat evaluations

We used the maximum entropy model (Maxent version 3.3.3 k; Phillips et al., 2006; http://www.cs.princeton.edu/wschapire/Maxent/). For each species, 75% of the location point data were used as a training model, and the remaining 25% for validating the Maxent model. The algorithm runs either 1000 iterations of these processes or continues until convergence (threshold 0.00001). The outputs were transformed into raster format using the ArcMap tool in ArcGIS software for further analysis.

To calibrate and validate the robustness of evaluation for the Maxent model, threshold-independent receiver-operating characteristic (ROC) analyses were used. An area under the receiver-operating characteristic curve (AUC) was examined for additional precision analyses. The Jackknife test was used to assess the relative importance of the variables. The final potential species distribution map had a range of values from 0 to 1 which were regrouped in to four classes of potential habitats viz., 'high potential' (>0.6), 'moderate potential' (0.4 – 0.6), 'low potential' (0.2 – 0.4) and 'not potential' (<0.2).

After using the current climatic data to model the spatial extent of suitable habitat for *P. delavayi* and *P. rockii*, modeling projections were performed for four future climate scenarios (RCP2.6–2050, RCP2.6–2070, RCP8.5–2050, and RCP8.5–2070) to predict the extent of suitable habitat for those two species in the future. Future habitat polygons were classified as (i) become suitable, (ii) become
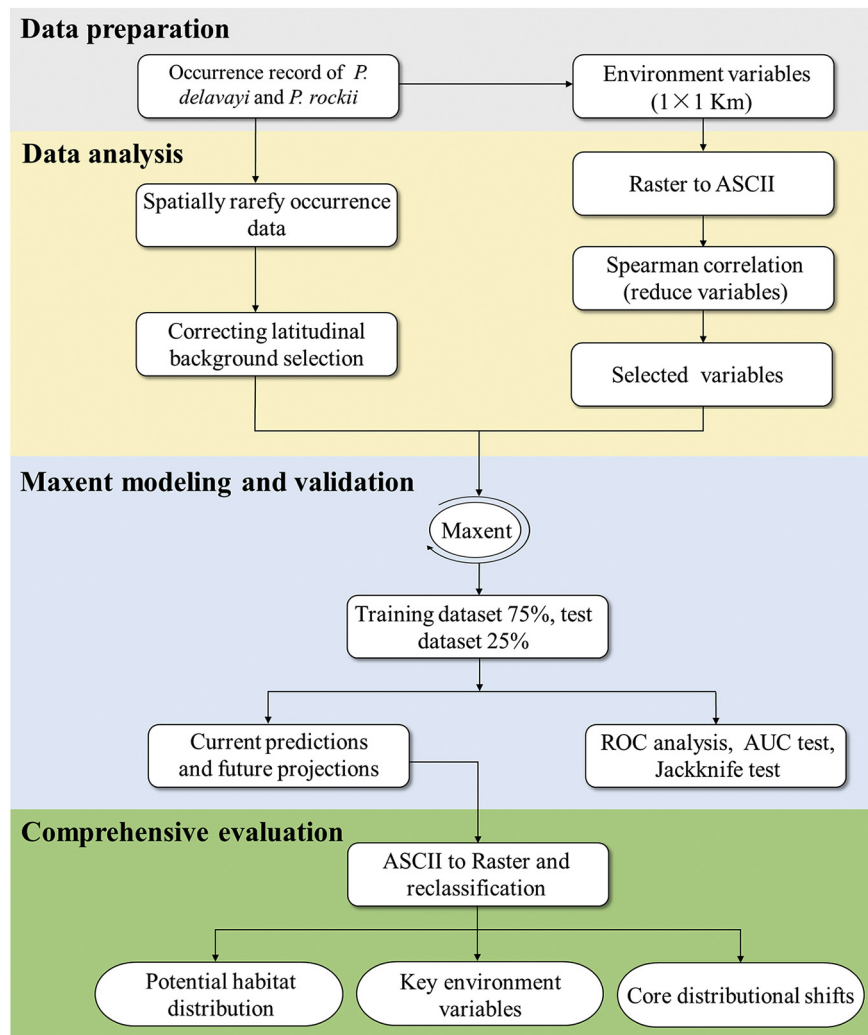
Data preparation

```
Occurrence record of  P.          Environment variables
  delavayi and P. rockii              (1×1 Km)
```

Data analysis

```
Spatially rarefy occurrence          Raster to ASCII
         data

                                 Spearman correlation
                                  (reduce variables)

 Correcting latitudinal
 background selection             Selected  variables
```

Maxent modeling and validation

```
                    Maxent

            Training dataset 75%, test
                 dataset 25%

 Current predictions             ROC analysis,  AUC test,
 and future projections              Jackknife test
```

Comprehensive evaluation

```
          ASCII to Raster and
            reclassification

 Potential habitat     Key environment     Core distributional shifts
   distribution          variables
```

Fig. 1. Processing methodology in flow diagram.

unsuitable, and (iii) unchanged suitable; next, the spatial extents of regions in these three classes were calculated and illustrated.

2.4. The core distributional shifts

The trends of change in suitable area were also calculated and the centroids were compared for current and future suitable areas using SDM tool-box, a type of python-based GIS software (Brown, 2014). The present study focused on providing a summary of the core shifts in the distribution of *P. delavayi* and *P. rockii*. This was done by reducing the distribution of these species to a single centroid (central) point and creating a vector file that was used to depict the magnitude and direction of the predicted change over time. Lastly, we examined the shifts in distribution by tracking how the centroid changed with different SDMs.

3. Results

3.1. The species distribution model and its accuracy

Models for the *P. delavayi* and *P. rockii* performed better than random, with the given set of training and test data. The AUC training values were 0.983 and 0.966, respectively, indicating both models performed well and generated excellent evaluations. Currently highly suitable habitat areas for *P. rockii* were evaluated to occur in south Gansu, south Shanxi, north-east Sichuan and north Hubei provinces (Fig. 3A).

The evaluated areas of moderate suitable habitat included west Henan, central Shanxi, central to south Shaanxi. The current areas of moderate and highly suitable habitat for *P. rockii* encompass ca. 4.46 × 10^5 km^2. In *P. delavayi, the* highly suitable habitat areas were evaluated to occur in north-west Yunan Province, Garzê Tibetan Autonomous Prefecture of Sichuan Province, and a sporadic distribution in Linzhi of Tibet. The evaluated areas of moderate suitable habitat included north Yunnan, south-west Sichuan and south-east Tibet. The current areas of moderate and highly suitable habitat for *P. delavayi* encompass ca. 1.89 × 10^5 km^2.

3.2. Important environmental variables

The Maxent model's internal jackknife test of factor importance showed that temperature seasonality (Bio4, 32.3% of variation), isothermality (Bio3, 19.5% of variation), wet-day frequency (WET, 13.2% of variation) and mean UV-B in the lowest month (UVB-4, 11.8% of variation) made the greatest contributions to the distribution model for *P. delavayi* relative to other variables. The cumulative contributions of these factors reached values as high as 76.8% (Table 1). UVB-4 (39.3% of variation), annual precipitation (Bio12, 22.8% of variation), ground-frost frequency (FRS, 10.9% of variation) and vapor pressure (VAP, 8.3% of variation) made the greatest contributions to the distribution model for *P. rockii*. The cumulative contributions of these factors reached values as high as 81.4% (Table 1).
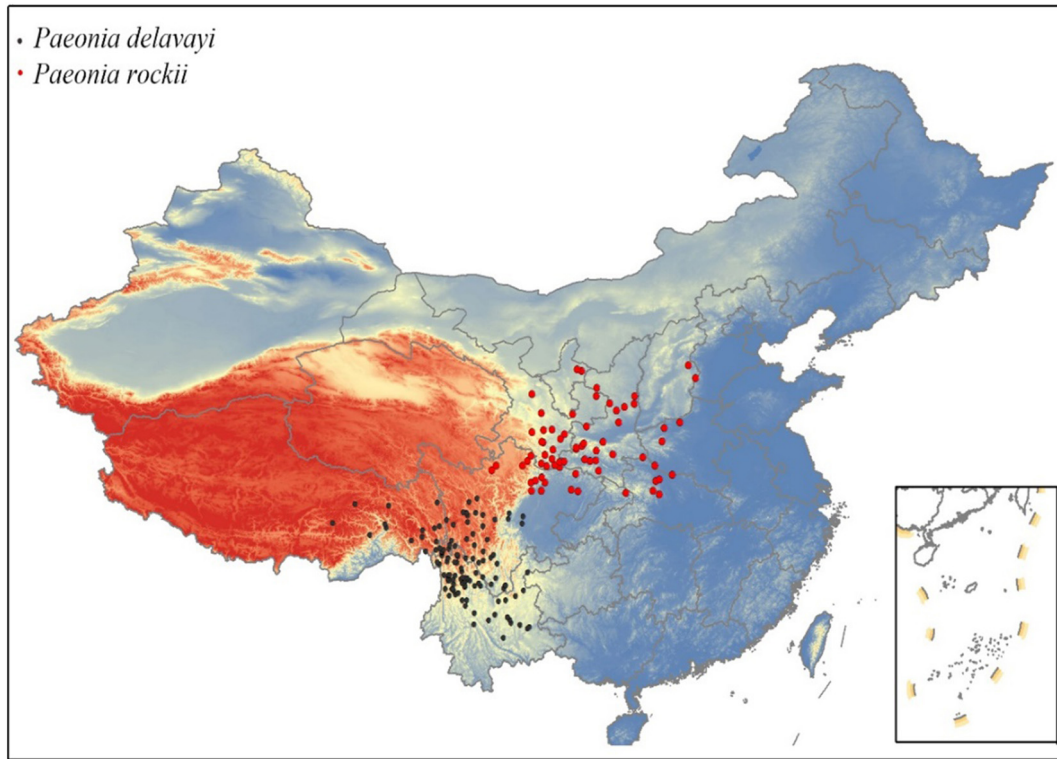
Fig. 2. Distribution records of *Paeonia delavayi* and *Paeonia rockii* in China.

Using the response curve (Fig. 4), we obtained the thresholds (existence probability > 0.2) for the main bioclimatic parameters. In *P. delavayi*, temperature seasonality (Bio4) ranged from 3955 to 6222, isothermality (Bio3) ranged from 42 to 51, wet-day frequency (WET) ranged from 77 to 138, and mean UV-B in the lowest month (UVB-4) ranged from 2115 to 3342 J·m^{-2}·day^{-1}; and in *P. rockii*, UVB-4 ranged from 782 to 1500 J·m^{-2}·day^{-1}, annual precipitation ranged from 390 to 1565 mm, ground-frost frequency ranged from 18.3 to 111, and vapor pressure (VAP) ranged from 23 to 94 hPa.

3.3. Future changes in suitable habitat area

Under RCP2.6–2050 climate scenario, Maxent predicted *P. delavayi* gains in suitable habitat area in the middle Sichuan, west Guizhou, central Yunnan, and east Tibet (Fig. 5-A1 and -B1; Table 2), amounting to ca.

2.03 × 10^5 km^2. The area of suitable habitat that was lost was ca. 3.40 × 10^4 km^2 and was predicted for the north of Tibet and central Sichuan (Fig. 5-A1 and -B1; Table 2). Under RCP2.6–2070 climate scenario (Fig. 5-A2 and -B2), the increased and decreased habitat stayed the same with 2050, the highly suitable area increased from 0.68% to 1.24% and the not suitable area from 95.16% to 94.09% (Table 3).

In *P. rockii*, Maxent predicted gains in habitat area in the north of Shanxi and Guizhou, north-west of Hubei, south-west of Hebei, central Henan and Sichuan under the 2050 scenario (Fig. 5-C1 and -D1), amounting to ca. 4.02 × 10^5 km^2. The area of suitable habitat lost was ca. 3.80 × 10^4 km^2, predicted for central Shananxi (Fig. 5-C1 and -D1; Table 2). Overall, we saw a restricted range expansion of suitable habitat area. Under RCP2.6–2070 climate scenario, the increased habitat was continuing to increase and most of Henan became low suitable habitat for *P. rockii* (Fig. 5-C2 and -D2). The low suitable habitat increased

Table 1

Percentage contributions and permutation importance of the bioclimatic variables included in the Maxent models for *Paeonia delavayi* and *Paeonia rockii*. Variables without any values (indicated by ×) were removed because of high cross-correlations.

Symbol	Bioclimatic variables	Paeonia delavayi		Paeonia rockii	
		Contribution (%)	Permutation importance	Contribution (%)	Permutation importance
BIO1	Annual mean temperature	0.4	10.6	×	×
BIO2	Mean diurnal range	0.5	16.3	1.2	1.4
BIO3	Isothermality	19.5	3.3	0.1	0.8
BIO4	Temperature seasonality	32.3	7.1	2.8	19.4
BIO6	Min temperature of coldest month	×	×	1.7	9.6
BIO12	Annual precipitation	3.4	2.3	22.8	24.1
BIO15	Precipitation seasonality	0.6	19.4	4.5	1.1
FRS	Ground-frost frequency	0.4	5.7	10.9	4.5
GDD	Growing degree days	3.4	1.7	0.5	1.2
SC	Soil organic carbon	0.2	1	0	1
SpH	Soil pH	2.3	4.1	0.7	2.5
VAP	Vapor pressure	1.6	2	8.3	2.9
WET	Wet-day frequency	13.2	13	6.8	13.3
UVB1	Annual mean UV-B	6.4	3.1	0.1	0
UVB2	UV-B seasonality	3.9	4.5	0	0
UVB3	Mean UV-B of lightest month	0.1	0.6	0.2	0.1
UVB4	Mean UV-B of lowest month	11.8	5.3	39.4	18.1
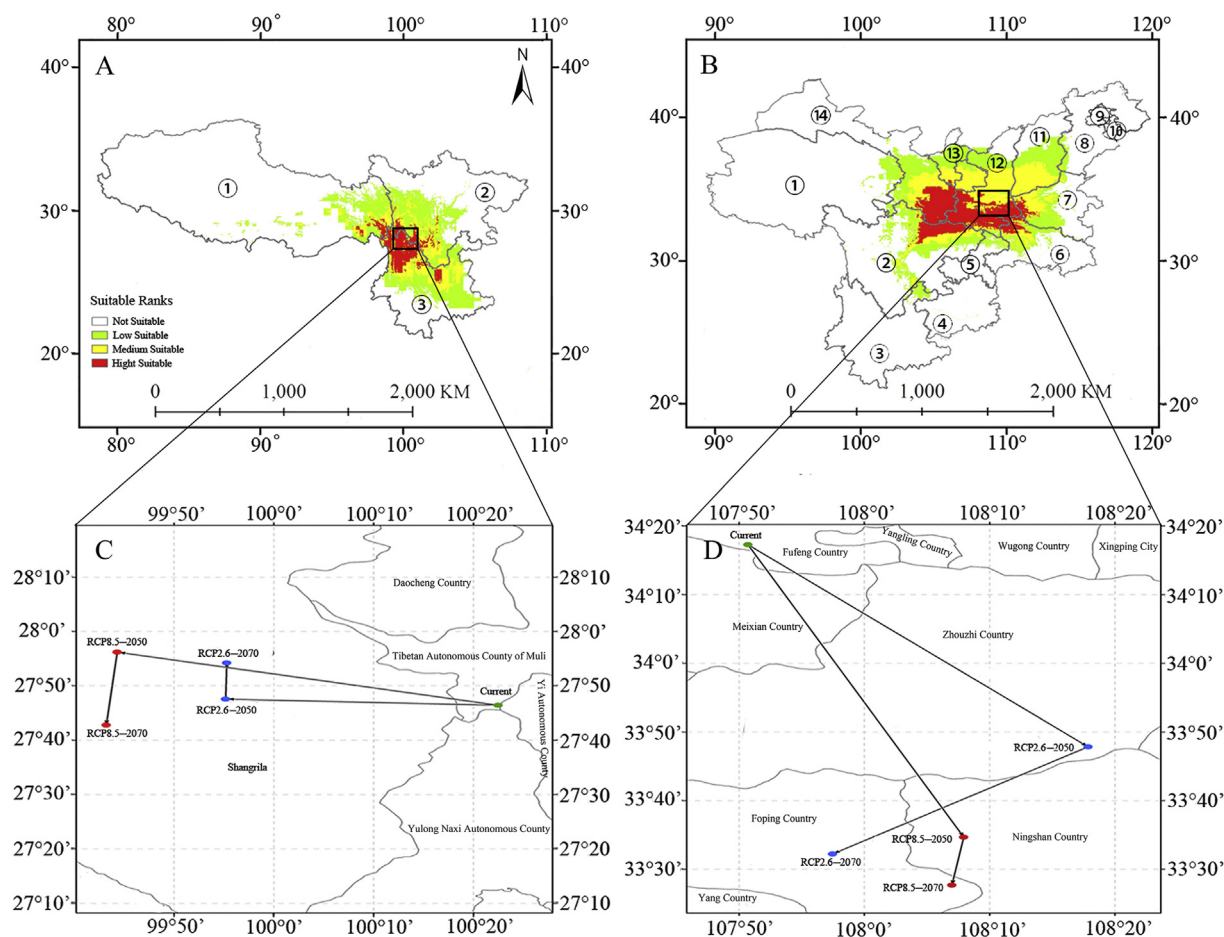
Fig. 3. Predicted current distribution model (A, B) and the core distributional shifts (C, D) under different climate scenario/year for *Paeonia delavayi* (A, C) and *Paeonia rockii* (B, D). Arrow indicates magnitude and direction of predicted change through time. ① Qinghai; ② Yunnan; ③ Sichuan; ④ Guizhou; ⑤ Chongqing; ⑥ Hubei; ⑦ Henan; ⑧ Hebei; ⑨ Beijing; ⑩ Tianjin; ⑪ Shanxi; ⑫ Shaanxi; ⑬ Ningxia; ⑭ Gansu.

from 3.91% to 9.40% but the moderate and highly suitable habitats changed little (Table 3).

Under the RCP8.5 climate scenario, Maxent predicted gains in suitable habitat area for *P. delavayi* by ca. 1.31×10^5 km² in east Yunnan and south-east of Tibet by 2050 (Fig. 5-A3 and -B3). The area decreased by ca. 4.30×10^4 km² in central Yunan by 2050 (Table 2). However, by 2070, the area that had increased by 2050 decreased to 5.57×10^4 south-east of Tibet (Fig. 5-A4 and -B4; Table 2). The area decreased to ca. 1.22×10^5 km² in central Yunnan, northwest of Tibet and southeast of Sichuan. Overall, we saw an increased pattern in unsuitable habitat. However, compared with the current time, high suitable habitat increased from 0.68% to 1.24% by 2070 (Table 3).

In *P. rockii,* the increased distribution area covered ca. 4.76×10^5 km² and occurred north of Shanxi, west of Hebei and Shaanxi and central to north of Guizhou in RCP8.5–2050 (Fig. 5-C3 and -C4; Table 2). The loss of suitable habitat was ca. 2.7×10^4 km² in central Shaanxi. However, the increased range decreased to $\times 10^5$ km² and the decreased range increased to 6.3×10^4 km² by 2070 (Fig. 5-C3 and -C4; Table 2). Overall, the portion of unsuitable distribution area decreased but the low suitable area increased (Table 3).

3.4. The core distributional shifts

The centroid of the current habitat of *P. delavayi* was located at the position of 100° 15′ E and 27° 46′ N in north-west Yunan Province (Fig. 3B). The centroid of suitable area shifted to 99° 77′ E and 27° 49′ N in the northwest under RCP2.6–2050 and to 99° 76′ E, 27° 72′ N under RCP2.6–2070. Under RCP8.5–2050, the centroid of future suitable

area was located at a northwest position (99° 44′ E, 27° 78′ N), but under RCP8.5–2070, the centroid of suitable area shifted to the southwest (99° 42′ E, 27° 43′ N). Overall, we saw that the core distribution shifted towards the west under both future emission trajectories in *P. delavayi* (RCP2.6, RCP8.5).

In *P. rockii,* the centroid of the current habitat was located at the position of 107° 55′ E and 34° 16′ N in south-west Shanxi Province (Fig. 3D). The centroid of suitable area shifted to 108° 17′ E, 33° 47′ N in the southeast under RCP2.6–2050 and to 107° 56′ E, 33° 37′ N under RCP2.6–2070. Under RCP8.5, the centroid of suitable area shifted to 108° 08′ E and 34° 35′ N by 2050 and to 108° 07′ E and 33° 28′ N by 2070.

4. Discussion

All wild tree peony species are endemic to China, and they are highly valuable resources (Hong et al., 2017). However, many wild peony plants have been overharvested for their roots, which can be used as a medicine. In this study, we performed a detailed analysis on the suitable habitat of two peony species under current and future climate scenarios which will function as an important step in formulating a feasible strategy for their conservation.

Paeonia delavayi has a wide distribution, including central and northwest Yunnan, southwest Sichuan, and southeast Tibet. Our model indicated that the moderate and high suitable habitat area encompassed ca. 1.89×10^5 km² for the species under current climate conditions and the center area was in northwest Yunnan. This model is in agreement with the precious study that found this species' range
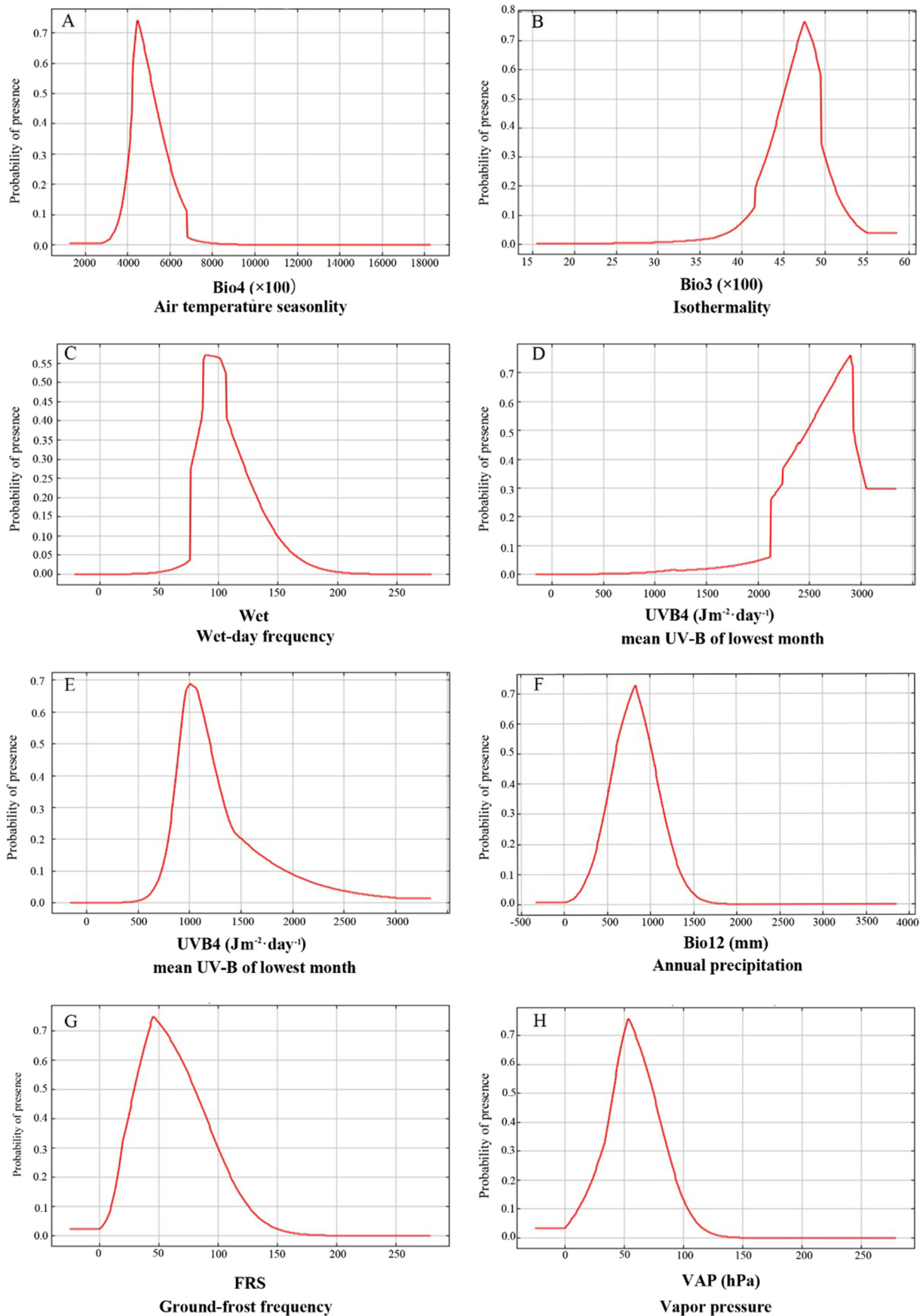
Fig. 4. Response curves for important environmental predictors in the species distribution model for *Paeonia delavayi* (A-D) and *Paeonia rockii* (E-H).
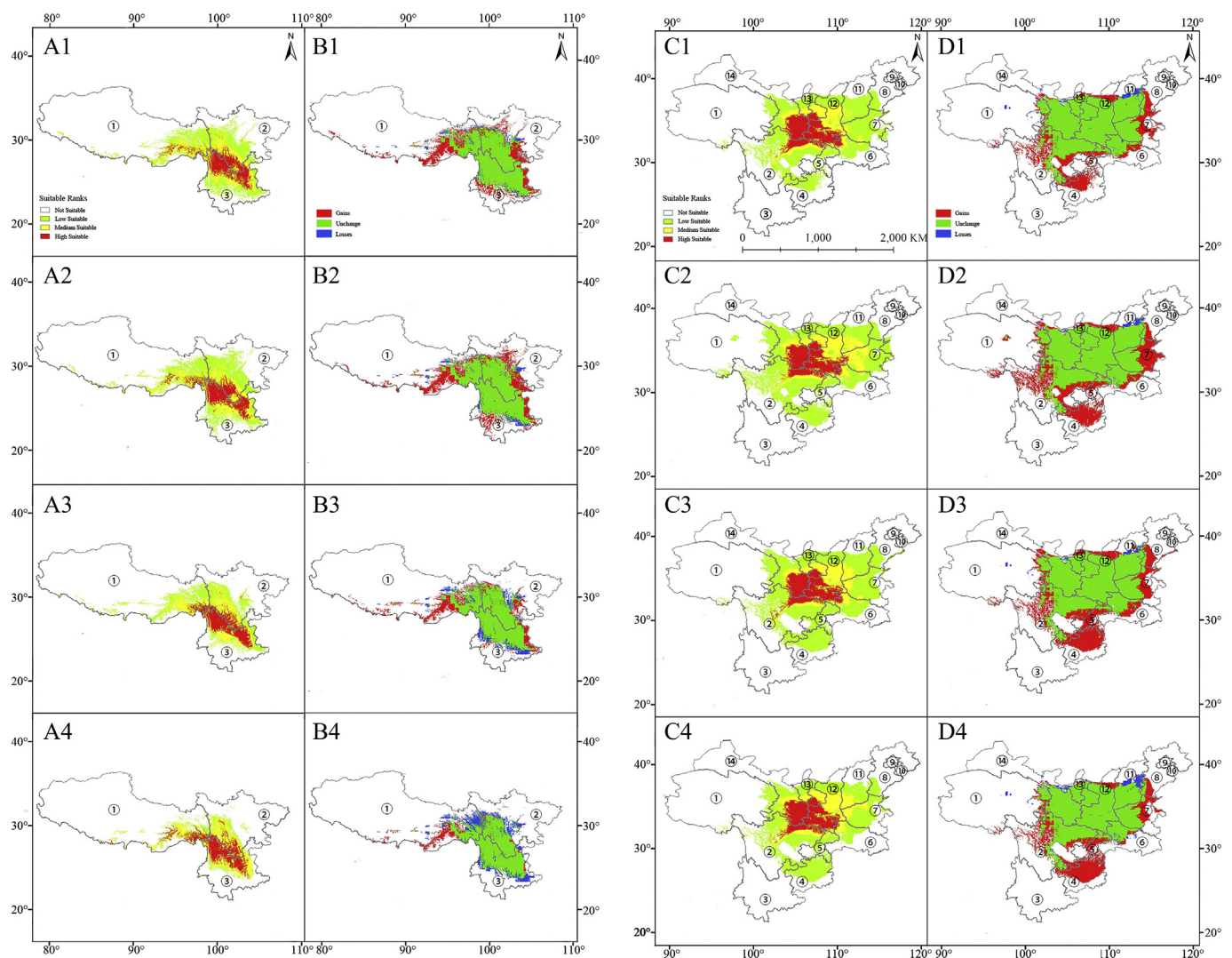
Fig. 5. Future species distribution models (SDMs) of *Paeonia delavayi* and *Paeonia rockii* under climate change scenarios RCP2.6 and RCP8.5. A, SDM for *P. delavayi*; B, Comparison between the current SDM and the SDM under future climate scenario for *P. delavayi*; C, SDM for *P. rockii*; B, Comparison between the current SDM and the SDM under future climate scenario for *P. rockii*; 1, future climate scenario RCP2.6 in 2050; 2, future climate scenario RCP2.6 in 2070; 3, future climate scenario RCP8.5 in 2050; 4, future climate scenario RCP8.5 in 2070. ① Qinghai; ② Yunnan; ③ Sichuan; ④ Guizhou; ⑤ Chongqing; ⑥ Hubei; ⑦ Henan; ⑧ Hebei; ⑨ Beijing; ⑩ Tianjin; ⑪ Shanxi; ⑫ Shaanxi; ⑬ Ningxia; ⑭ Gansu.

was from 24 to 32°N and 94 to 104°E (Hong et al., 2017). *P. rockii* has a wide but sporadic distribution in China. It is distributed in deciduous forest margins in Shananxi, Gansu, and western Henan provinces, ranging from 31°40′ N to 36°45′ N and 104°E to 112°E (Hong et al., 2017). Our modeling indicated that the moderate and high suitable area encompassed ca. 4.46×10^6 km² for the species under current climate conditions. Interestingly, some areas of Hubei, Qinghai, Shanxi and Sichuan provinces are also evaluated to be suitable, and this would provide areas for introducing *P. rockii* in the future.

Among the 17 environmental variables adopted in the model, temperature seasonality and isothermality made the greatest contributions to the distribution model for *P. delavayi* relative to other variables,

indicating that these factors play important roles in its distribution. With a decrease of temperature seasonality and an increase of isothermality, the possibility of *P. delavayi* distribute increased. This result is supported by the fact that the climatic characteristics of an area act as key elements for population regeneration (Hansen et al., 2018). Most of the distribution area of *P. delavayi* receives the influence of both Pacific and Indian oceans, has mild to warm winters, and warm summers (Zhang et al., 2006). The large isothermality ensures that *P. delavayi* can use the relatively high temperature to photosynthesis during the day, while the relatively low night temperature can decrease the energy consumption of respiration, which is beneficial for nutrient accumulation by its spindle-fleshy root system (Hong et al., 2017).

Table 2
Dynamics of changes in distribution area for *Paeonia delavayi* and *Paeonia rockii* under four future climate scenarios/years.

Area ($\times 10^5$ km²)	Paeonia delavayi			Paeonia rockii		
	Increased	Decreased	Unchanged	Increased	Decreased	Unchanged
RCP2.6–2050	2.04	0.34	4.22	4.02	0.38	7.97
RCP2.6–2070	2.03	0.40	4.16	5.65	0.28	8.07
RCP8.5–2050	1.31	0.74	3.82	4.77	0.43	7.92
RCP8.5–2070	0.56	1.22	3.34	3.97	0.63	7.72

Table 3

Portions of different classes of potential distribution area of *Paeonia delavayi* and *Paeonia rockii* under current and four future climate scenarios/years.

Portion of area (%)	*Paeonia delavayi*				*Paeonia rockii*			
	Not suitable	Low suitable	Moderate suitable	High suitable	Not suitable	Low suitable	Moderate suitable	High suitable
Current	95.16	2.87	1.29	0.68	91.46	3.91	2.83	1.80
RCP2.6–2050	94.03	3.06	1.72	1.19	87.83	8.21	2.08	1.88
RCP2.6–2070	94.09	3.07	1.60	1.24	86.07	9.40	2.66	1.87
RCP8.5–2050	95.10	2.18	1.54	1.18	87.14	8.73	2.26	1.87
RCP8.5–2070	96.28	0.84	1.64	1.24	88.16	7.51	2.46	1.86

Temperatures were reported to effect the vegetative growth (Li et al., 2012), flower bud differentiation (Philip, 2011), and seed dormancy and germination (Baskin and Baskin, 2014) of *P. delavayi*. Dormancy in peony seeds typically is complex, requiring sequential breaking of dormancy in roots and shoots (Andrieu et al., 2007). In seeds of most peony species, warm stratification (15–25 °C) breaks dormancy of the root, while cold stratification (0–10 °C) breaks the dormancy of epicotyl [See Baskin and Baskin, 2014 for a more detailed account of the results of the studies on seed germination in peonies]. However, the suitable temperature ranges for dormancy break of *P. delavayi* were 10–15 °C (Jing and Zheng, 1999). Temperatures > 20 °C were found to be unfavorable for seed germination, which would lead to a much longer time for germination and increase frequency of abnormal seedlings (Jing and Zheng, 1999). This suggests a physiological limit to the distribution of *P. delavayi*. A similar distribution pattern was recently reported for the *Fritillaria cirrhosa* (Liliaceae), for which isothermality was the variable with highest contribution (Wang et al., 2014). Future studies should focus on testing if other species distributions in this latitudinal range could reflect the influence of this climatic variable.

The most important bioclimatic features affecting the presence of *P. rockii* were UVB-4 and annual precipitation. UV-B has a significant influence on the subaerial organs of plants (Yang et al., 1994; Garcia-Corral et al., 2017). It induces morphological changes including thicker leaves (Wargent et al., 2009), shorter petioles (Robson et al., 2015), shorter stems, increased axillary branching (Hectors et al., 2007) and altered root/shoot ratios (Robson et al., 2015). UV-B usually interacts with increased CO_2 concentration, availability of nutrients, water stress and other environmental factors (Garcia-Corral et al., 2017) and those factors modulate the effects of UV-B (Wargent et al., 2009) which in turn may affect plant responses to other environmental parameters (Qaderi and Reid, 2005). Previous studies have shown that the photosynthesis, light saturation point and stomatal conductance of *P. rockii* are affected by micro-environment (Zhang et al., 2014). However, little is known about the effects of UV-B radiation on the physiology of peonies, and we recommend quantitative studies in the future.

Annual precipitation lower than 390 mm greatly reduces the probability of presence of *P. rockii*, indicating that precipitation is an important constraint to its distribution. Previous studies have shown that plant height, number of branches, leaf area and photosynthesis of *P. rockii* decreased significantly with a decrease of water availability (Ari, 2015). In addition, seedling emergence and growth of plant are directly affected by water availability (Baskin and Baskin, 2014). All of these hydrological factors may have played main roles in shaping the ecological adaptation of *P. rockii*, and have great impacts on the distribution of this species.

With global warming, some species will migrate to high latitude or high elevation (Root et al., 2003; Lenoir et al., 2008; Bertrand et al., 2011), while other species may adapt to these changes physiologically or phenologically (Hu et al., 2015). A study in Switzerland covering 26 mountains revealed that the alpine flora is expanding its range to higher elevations but is reaching the peaks (Grabherr et al., 1994). Consistently, our prediction showed that the shift in distribution of suitable habitat areas to high elevations would become gradually more significant. The centroid of suitable area of both *P. delavayi* and *P. rockii* shifted were

higher than current habitat (Ma, 1999; Zheng, 2016), which may be facilitated through adaptations.

Under the low concentration of greenhouse gas emissions scenario (RCP2.6), suitable habitat range of both *P. delavayi* and *P. rockii* will increase as global warming intensity proceeds (Table 3). Under the higher concentrations of the high greenhouse gas emissions scenario (RCP8.5), we predicted suitable habitat range of *P. delavayi* decreased while *P. rockii* increased. This trend is consistent with that of previous studies (Zhang et al., 2015; Ma and Sun, 2018), which indicates that temperature had a positive effect on *P. delavayi* and *P. rockii* by accelerating the process of phenology and prolonging the growing season. However, a continuous rise in temperature might had a negative effect on plants (Xu and Xue, 2013), which may differ between widely and narrowly distributed species. Plants with narrow distribution usually have a constrained ecological adaptability and are more susceptible to the impact of climate change than broadly distributed species (Zhang et al., 2015; Ma and Sun, 2018). The decrease of suitable habitat range of *P. delavayi* might be related to its narrow ecological adaptability. As discussed above, temperature was the most important factor shaping *P. delavayi* distribution and the suitable temperature ranges for dormancy break of *P. delavayi* were 10–15 °C (Jing and Zheng, 1999). A continuous rise in temperature would preclude regeneration from seeds (Walck et al., 2011).

Another consideration that will influence the distribution of both species is the future utilization pressure created by the increased use of these medicinal species when other plants fail to thrive under changed climates. As a result, increased use of some medicinal species may lead to extinction that occurs despite the presence of suitable habitats now and in the future (Svenning et al., 2009). Climatic and land use change will result in a decrease in the availability of suitable habitats. The present study suggests that *P. delavayi* and *P. rockii* will be broadly adaptable to future climatic conditions. However, large amounts of currently suitable habitat may disappear because of land use change and human use for economic purposes. Urbanized areas transect nearly all suitable habitats of both *P. delavayi* and *P. rockii*, and extensive areas of suitable habitat for these two species has already been urbanized or modified for agricultural use.

Additional studies will be needed to quantify the effects of anthropogenic actions on the ability of these two species to adapt to future climatic conditions. The modeling in the present study predicted suitable habitat for both species will probably shift their distribution to higher elevations. We recommend that land management agencies actively manage the conservation of tree peonies in the wild, provide funds for extensive surveys to study their current status, and then develop a reasonable management strategy and other measures designed to conserve these precious wild peonies.

5. Conclusions

Estimating how climate change will affect the distribution of peony species is of vital importance for conservation. Our results indicated that the suitable habitat for *P. delavayi* and *P. rockii* tend to increase under the scenario for a low concentration of greenhouse gas emissions (RCP2.6), however, under the scenario with higher concentrations of emissions (RCP8.5), we predicted the suitable

habitat range of *P. delavayi* decreased while *P. rockii* increased. The projected spatial and temporal pattern of range shifts for *P. delavayi* and *P. rockii* will be a useful reference in developing forest management and conservation strategies for those two ecologically important species.

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